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GERMINAL ANALYSIS THROUGH HYBRIDIZATION.

By GEORGE HARRISON SHULL.

(Read April 23, 1910.)

The study of the various characteristics of plants and animals as independent units has made hybridization a valuable instrument in experimental morphology, and has given to the name of Mendel an enduring place as a true prophet in the history of biological progress.

The importance of the Mendelian contribution can scarcely be over-estimated. Before the "re-discovery" a decade ago, no one but Mendel had given an approximately correct interpretation of the composition and behavior of hybrid progenies, and the process of hybridization was therefore of no particular consequence for general biology. The *hybrid individual* was taken as the unit and comparisons between the hybrids and their parents were made in generalized terms involving the general aspect or *tout ensemble*. As only rarely were all the characteristics of either parent recombined in one of the offspring, the phenomena of segregation and recombination were considered of relatively rare occurrence, and described in terms of atavism or "throwing back" to the ancestral condition.

An important cause for the long delay in the discovery of the Mendelian phenomena was the distinction made between the offspring of species-crosses, which alone were distinguished as "hybrids," and the cross-bred offspring of more closely related forms, which were stigmatized as "mongrels." The difficulty of making species-crosses, the consequent rarity of such hybrids, and the usually uniform type of the offspring produced, all gave the impression of their greater scientific importance at a time when rarity and uniformity of phenomena instead of their general occurrence and variability seem to have made the stronger appeal.

Koelreuter, the first hybridologist, started the current in this direction by devoting his attention so strongly as he did to the phenomenon of sterility in hybrids, which he considered an important test of the specific distinctness of the parents. The very fact of fertility in the progeny of a cross seemed in later years to terminate its interest for him and only in rare instances in his writings do we find any data as to the characteristics of individuals belonging to second and later generations.

Gaertner dealt with the subject of hybridization in a much broader way and arrived at many interesting generalizations. However, he also worked almost wholly with species-crosses, purposely choosing his material with as wide differences as possible in order to facilitate definiteness of descriptions, but in this very effort to gain definiteness, the opportunity for studying the second and later generations was usually lost through the sterility of the first generation hybrids. He did, however, make some studies on such well-known Mendelian material as peas, sweet peas and Indian corn, but only in the last did he study a second generation, and in this the complexities introduced by "xenia" were doubtless the chief cause of his failure to find the simple law of segregation.

Practically all other hybridizers from Gaertner's time on to the beginning of the present century, considered the mere securing of hybrid individuals and their systematic description as the matters of prime value. Thus it was that the *combination* phenomena of hybridization alone occupied the stage, and the separation of the parental characters and their recombination in different individuals was only imperfectly recognized as variability and returns to one or other of the two parental types.

Two French investigators, Godron and Naudin, who were working synchronously with Mendel, seem to have come very near sharing Mendel's great discovery, but each of these two investigators by a strange chance observed a different phase of the Mendelian phenomena, Godron reaching the conclusion that in mongrels ("métis") all progenies return in several generations to the parental types and then breed true, while Naudin thought he had demonstrated that the progenies continue to vary after the F_2 and

never become fixed. However, in the work of Godron and Naudin, their near discovery of Mendelian segregation was not due to a deliberate consideration of the various characteristics as units, but rather to the fact that several of the forms which they used in their cultures, differed from each other by single unit-characters, as exemplified for instance by the purple color of stems in *Datura Tatula*, contrasted with the green stem of *D. Stramonium*, or the usual prickly fruit of the *Daturas* contrasted with the smooth fruit of a var. "*capsulis inermibus*."

The Mendelian method of following single characteristics possessed by the parents, not only into their F_1 progeny, but also through the second, third, and later generations, brought to light a regularity of behavior which has served to shift the stress from the simple combination phenomena involved in hybridization, to the phenomena of separation and recombination of such elementary differences as existed between the two parents.

The result of this important innovation of method has been to demonstrate beyond a peradventure, that many of the distinguishing characteristics of adult plants and animals are predetermined by corresponding differences in the constitution of the germ-cells; that these differences may be of an elementary character, capable of separation into different germ-cells; that when two parents used in any cross, differ by such elementary characters, half the resultant germ-cells have the capacity to produce any given elementary character of the one parent, the other half possess the capacity for the production of the corresponding or alternative characteristic of the other parent; that as a rule such unit-characters are wholly independent from one another and capable of rearrangement in every possible combination with one another; and, finally, that it is purely a matter of chance, which available type of sperm shall fertilize any given egg.

The separation of the unit-characteristics into different germ-cells in every possible combination with other characteristics gives the power in many cases to recognize all the unit-differences which served to distinguish the two parents. By the study of the hybrid progenies we are thus given an insight into certain phases of the

protoplasmic constitution and the "mechanism" of heredity, which has been totally unattainable by other means.

In making analyses of such hybrid progenies and in working out the nature and delimitations of the unit-differences involved in Mendelian crosses, no assumption need be made as to the ultimate nature of the "genes"¹ or determiners. The attitude of nearly all experimenters in the field of genetics is one of more or less consciously suspended judgment on this point, and I believe that no other attitude is justified at the present time. So far as I am aware no investigator of the Mendelian phenomena "sees only particles" as Dr. Riddle² has erroneously assumed, although it must be confessed that his speech does sometimes seem to symbolize them. The Mendelian interpretations do not "stand as a formidable block in the path of progress," nor as any block at all, since all terminology is more or less symbolic, and comes to mean new things as rapidly as new truths are brought to light. All investigators in this field will be appreciative of the service Dr. Riddle has performed in bringing to their notice the recognized facts in the process of melanin formation, though they can scarcely fail to regret his unfamiliarity with the present state of genetic science, and with the attitude of those engaged in the investigations. If he had been thus familiar with work in genetics, he might very easily have shown that the facts of melanin chemistry are in harmony with the mass of other data for which the "Mendelian interpretation" has proved so illuminating.

Although the question of epigenesis *versus* preformation is emphasized as a fundamental difference between Riddle's views and those of the Mendelians, this supposed difference is mainly imaginary. Riddle's assumption of different "strengths" in the germ-cells as a possible method of accounting for the production of different colors or other characters in adult animals, involves a preformation of the same order as that assumed by the investigators of

¹ The genes are the differences, of whatever nature, whose existence in the germ-cells determines the capacity of the unit-characters to be present or absent in the individuals developed from those germ-cells.

² Riddle, O., "Our Knowledge of Melanin Color Formation and its Bearing on the Mendelian Description of Heredity," *Biol. Bull.*, 16: 316-351, May, 1909.

Mendelian phenomena. Every thremmatologist is too familiar with the facts of ontogeny to give the slightest credence to anything approaching the old embôtement hypothesis, but he must accept as a philosophical necessity the fact that there can be no action without an agent. There can be no "strength" without something to be strong. Preformation and epigenesis are simply inseparable phases of a single philosophical unity and any attempt to separate them is fallacious.

The statement that the "nature of present Mendelian interpretation and description inextricably commits to the 'doctrine of particles,'" presents Mendelism and its investigators in a false light, as no such commitment is involved. Despite the enormous activity and splendid progress that has been made in these ten years in tracing the Mendelian behavior until it has become evident that it is a well-nigh universal phenomenon,—no doubt practically co-extensive with sexual reproduction,—the changes in descriptive terminology to which Dr. Riddle deprecatingly refers, have been remarkably slight, and one reads Mendel's original account with wonder that it should still be so modern. Mendel's genius grasped the essentials of this type of inheritance so completely and presented it with such fulness and clarity, that it may doubtless always serve as a good elementary presentation of the subject. But while Mendel's paper is in such essential accord with "present interpretation" as to seem strictly modern, there occurs throughout his whole admirable discussion, not one word of suggestion that he attributes the occurrence of any external character to the presence of an internal particle.

Modern Mendelians as a rule have specifically declined to postulate the presence of material "particles" as the physical bases of unit-characters. Bateson, who has done more than any other to demonstrate the wide applicability of the Mendelian method, clearly placed himself from the first in opposition to any purely morphological interpretation of Mendelian phenomena by giving to his reports to the evolution committee the title: "Experimental Studies in the *Physiology* of Heredity," and he has from first to last carefully guarded all statements with reference to the nature of the genes, in such manner as to be entirely non-committal. Other investigators have either wholly ignored the question, or have usually

couched their suggestions in such terms as to show that they were open to any new light upon the subject.

Although I have never looked upon the Weismannian conception of character-determiners as at all plausible, I do not agree with Dr. Spillman³ that the facts presented by Riddle "*disprove*" the "particle hypothesis." The only manner in which Riddle despatched(?) the "particle hypothesis" was by ruling the observed facts of Mendelian heredity out of court. If the Mendelian phenomena are real, and no one can do careful investigation in this field without becoming convinced that they are, the postulation of "particles" or "bullets" having certain chemical and physiological properties, and behaving during the reproductive process in some such manner as the cytologists are fairly agreed that the chromosomes behave, would offer a complete explanation, and the correctness of such an explanation can not be *disproved* except by proving that some other method of determination is the true one. However, while the particle hypothesis is not disproved, I have no doubt that the Weismannian, and perhaps also the De Vriesian conception of the genes will seem less and less plausible as new facts accumulate.

In Dr. Spillman's⁴ brilliant development of what he calls the "teleone hypothesis," a suggestion is offered which virtually makes the chromosomes the "bullets" whose differential properties determine the unit-characters. This interpretation of the Mendelian phenomena has much to commend it, especially as it calls for no structure and no type of behavior which are not already generally recognized as being universally present in the formation of the germ-cells, and it has the added advantage that it seems to be capable of experimental tests.

I can not see, however, that Dr. Spillman has presented "an explanation of Mendelian phenomena without resorting to the idea of unit-characters." If he appears to do so, it is only because he gives to them a new name. The unit-characters are the empirical phenomena for whose explanation the "bullets," "teleones" or genes of any other sort, are devised. It is no new idea that these

³ In conversation.

⁴ Spillman, W. J., "Mendelian Phenomena Without De Vriesian Theory," *Amer. Nat.*, 44: 214-228, April, 1910.

unit-characters are "differentials," as this was recognized by Mendel himself and has been common knowledge to all investigators of Mendelian heredity since.

The length of hair in guinea-pigs and rabbits, the stature of peas, sweet peas, beans, etc., the length of styles in *Primula* and *Oenothera*, density of the heads in wheat and barley, and in fact practically all other characters with which Mendelian investigators have worked, have been so obviously differentials that it is impossible to assume that any Mendelian has ever meant anything else by the expression, "unit-character."

This being true, the contention of Riddle that even in the absence of a given unit-character there is not a complete absence of the particular manifestation in which the essence of that unit-character consisted, or in other words, that the unit-character is simply a phase or "strength" of some "rather general protoplasmic power," is not likely to seriously disturb the Mendelians, since that is a fact with which they have long been familiar.

It appears to me that the unnecessary shifting of the terminology of clearly distinguishable empirical phenomena is undesirable. The unit-characters are *real things* capable of repeated demonstration. They are still differential *characters*, and possess the capacity to behave as *units*, entering into various combinations with other unit-characters and capable of reëxtraction from them, or of being absent altogether, regardless of the manner in which their behavior is explained. The genes, on the other hand,—the ultimate organs of the protoplasm or conditions of the protoplasmic substance upon whose existence depends the capacity to give certain series of reactions, or to pass through certain cycles of ontogenetic development,—are purely inferential. Their nature is not yet capable of demonstration. They are "unknown gods" to whom each new prophet may appropriately apply a new name whenever he ascribes to them new attributes.

While the ultimate nature of the genes lies wholly beyond the powers of present-day analysis, and there is nothing therefore to warrant a departure from the prevailing attitude of suspended judgment, the more intimately the unit-characters themselves are studied, the better will be the basis provided for an understanding of their

common properties, and thus finally for an approximation to the nature of the genes which determine them.

The most hopeful directions of approach in the effort to learn more of the true inwardness of the unit-characters, are those of chemical analysis and experimental cytology. As applied to unit-characters, these are almost untouched fields at present, though several investigators have made a beginning. Miss Wheldale, especially, has made a hopeful beginning in the investigation of the chemistry of anthocyanin colors which have continually exhibited typical Mendelian behavior. Several unit-characters which have been recognized and described heretofore only in terms of color-factors, now seem to be capable of description in terms of a chromogen (present in all sweet peas and stocks investigated), and of activators, peroxidases, peroxides, and reducers, thus making the various colors "the result of definite oxidation stages of the chromogen." Riddle has come to much the same conclusion in regard to the nature of the melanin colors, from a consideration of the work of Bertrand, Gessard, Spiegler and others.

In experimental cytology there seems to have been nothing done as yet, which can throw light on the nature of those unit-characters involving the structure and size of parts. How are the number and direction of cell-divisions that shall take place in any cell-lineage determined? Are these also referrable to the presence of definite chemical substances or to definite configurations of protoplasmic molecules? To these questions I believe no satisfactory answer is now possible, but that these processes are controlled in many instances by characteristics possessed by the germ-cells, rests upon abundant experimental evidence.

While waiting for further information from the chemist and the cytologist, there is still abundant room for the work of the experimental breeder. Owing to the characteristic distribution of the genes at the time of germ-cell formation already described, Mendelian hybridization provides a partial analysis of the germ-plasm, and thus gives some insight into the constitution of living protoplasm. It is of great importance that such analysis be continued until all the unit-differences of plants and animals have been studied,

for only when this is done can the full scope and significance of the Mendelian phenomena be understood.

It need scarcely be pointed out that the complete tracing of the germinal analysis which takes place in Mendelian hybrids, is attended with many difficulties. The unit-characters represent capacities for reaction in a certain, very specific way to given conditions of environment. Individuals having the same unit-composition may react in a totally different way to a different environmental complex. Some unit-characters are so sensitive to slight differences of environment that they offer a wide range of fluctuation, or they may represent such a slight differential as to be readily distinguishable only in their plus-fluctuations. Two or more unit-characters may even be indistinguishable from one another as Nilsson-Ehle⁵ has shown to be the case in certain unit-characters of wheat and oats, and East⁶ in endosperm colors of corn. Many unit-characters are quite invisible except when occurring in combination with some one or more other characters, and this fact has led to what is called the "factor hypothesis." That the factors are real unit-characters, differing in no essential way from ordinarily visible unit-characters, is now in a fair way to be demonstrated by such work as that of Miss Wheldale, and others who are working along similar lines. The implication by some writers that the factor hypothesis is a late development of Mendelism is not correct, as Mendel himself suggested it tentatively. The difficulty of tracing invisible characters necessarily made the development of knowledge regarding them slower than that regarding the easily visible characters, but the essential correctness of Mendel's suggestion has been abundantly substantiated.

All of the foregoing difficulties can be overcome, and are continually being overcome by careful analysis and patient, long-continued breeding tests.

Finally, since we are examining the Mendelian process as one of germinal analysis it is appropriate to discuss for a moment the

⁵ Nilsson-Ehle, H., "Kreuzungsuntersuchungen an Hafer und Weizen," 4to, pp. 122, 1909, Lund: Hakan Ohlsson.

⁶ East, E. M., "A Mendelian Interpretation of Variation that is Apparently Continuous," *Amer. Nat.*, 44, 65-82, Feb., 1910.

"insoluble residue." Although Mendelian behavior has proved to be nearly universal in those sexually produced plants and animals which are capable of breeding together normally, there are certain clear limitations to the process of analysis. Several instances are known in which differential characters are not segregated, and no analysis takes place with respect to these characters, even when most of the differential characters of the same plants or animals Mendelize in a perfectly typical manner. The relative frequency of this type of behavior may be greater than is now supposed but so far as clear evidence is available permanently blended inheritance of this type is relatively rare except in species-crosses, and in these latter the data is usually too scanty for safe generalization.

Aside from these cases which show a distinctly non-Mendelian mode of inheritance, it must be remembered that Mendelian analysis can be made only in the presence of differential unit-characters possessed by individuals *capable of life and of sexual reproduction*, and that therefore, there can be no test, except under rare circumstances, of the Mendelian nature of the more fundamental vital characters. This leaves it an open question whether the whole of the germ-plasm is a complex of such genes as those which give rise to the phenomena of unit-characters, or whether, with its wonderful general powers of assimilation, growth and reproduction, it consists of a great nucleus of which the genes are relatively superficial structural characteristics.

However, although nothing inconsistent with life and reproduction are ordinarily amenable to Mendelian analysis, this need not detract from the fundamental importance of unit-characters in the study of heredity and evolution, for the phenomena appearing in these fields are subject to exactly the same limitations. All that we know about heredity and evolution *must start* with a plasma capable of life and reproduction.

While thus leaving the absolutely fundamental characteristics of living matter untouched, the Mendelian method and its results have brought into harmonious relations many of the most diverse phenomena of phylogenetic differentiation and it is only fair to assume that they hold still greater promise for the future.